



Original research article

Seed dispersal effectiveness by greater one-horned rhinos and domestic bovids of a megafaunal fruit

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ABSTRACT

The extinction of megafauna, such as rhinos, from tropical Asian forests may have detrimental effects on the regeneration of plant species that rely heavily on their dispersal services. Understanding the potential of other animals to substitute the ecological function of megafauna is important for predicting ecosystem change following declines or extirpation of megafauna. Anthropogenic activities have led to the presence of domestic bovids in many tropical habitats, and these animals could be capable of substituting seed dispersal roles of megafauna. Here, we conducted feeding trials, germination tests, and collected movement data on greater one-horned rhino (*Rhinoceros unicornis*) and domestic bovids (*Bos primigenius*; *Bubalus bubalis*) in the national parks of Chitwan and Shuklaphanta, Nepal. Our aim was to investigate whether domestic bovids can serve as effective substitutes for rhinos in dispersing the megafaunal-fruited *Mallotus nudiflorus*, which are specialized for rhino dispersal. Specifically, we assessed the long-distance seed dispersal capabilities of rhinos and bovids by combining gut passage times and movement patterns. Additionally, we compared the seed germination success rates among rhinos, bovids and other dispersal modes (e.g., deer and water dispersal). We found that rhinos dispersed 80 percent of seeds over distances greater than 1 km, with potential dispersal distances of up to approximately 5.4 km within their maximum gut passage time. In contrast, cattle dispersed 20 percent of seeds over 1 km, with a maximum distance of around 2.2 km, while buffaloes dispersed 15 percent of seeds over 1 km, with a maximum distance of around 1.4 km. Seeds consumed by rhinos exhibited similar or better germination rates compared to seeds retrieved from cattle and buffalo dung, as well as other dispersal modes. These findings indicate that rhinos provide a

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functionally unique dispersal service for this megafaunal fruit, especially in long-distance dispersal. While domestic bovids can partially substitute the seed dispersal functions of rhinos, they cannot fully compensate for the loss of seed dispersal that occurs with the disappearance of rhinos.

1. Introduction

Wild ecosystems across the world have been transformed dramatically over the past centuries. Many habitats were occupied previously by several megafaunal species (defined here as animals weighing >1000 kg, Owen-Smith, 1988; Moleon et al., 2020), performing diverse functions, such as seed dispersal, herbivory and nutrient transfer, which were essential for maintaining ecosystems (Campos-Arceiz and Blake, 2011; Malhi et al., 2016; Galetti et al., 2018). Present-day wild ecosystems are fragmented and more often support a single (or no) megafaunal species due to extensive global and local extinctions of megafauna (Dirzo et al., 2014; Galetti et al., 2018). Domestic bovids frequently coexist in habitats with megafauna, either as feral or free-ranging domestic animals (Dahal et al., 2023, Young et al., 2018). Their presence can have a range of effects on ecosystems ranging from negative to positive (Mazzini et al., 2018). Due to their large body sizes and herbivorous diet, domestic bovids can perform similar ecological roles as megafauna. This suggests that they may play a role in ecosystem maintenance and provide functional redundancy in cases where megafauna have declined (Mazzini et al., 2018; Sekar et al., 2015; Young et al., 2018).

Megafauna are important seed dispersers for some fruit-bearing plants (Dinerstein and Wemmer, 1988, Sekar and Sukumar, 2013; Ong et al., 2022; Tan et al., 2021; McConkey et al., 2022a), because they can disperse many seeds from a wide range of sizes and across exceedingly long distances, which has positive impacts on the meta-population dynamics of plants (Campos-Arceiz et al., 2008; Poulsen et al., 2018, 2021, Fedriani et al., 2023). In comparison, smaller animals usually disperse seeds shorter distances, because of limited gut retention times and ranging behaviour (Ruxton, and Schaefer, 2012; Zwolak and Sih, 2020). The smaller gape-sizes of non-megafaunal animals can also result in mastication of larger fruits and seeds; for bovids and other ruminants the complex gut results in especially harsh seed handling and only very hard or very small seeds tend to survive consumption (Sridhara et al., 2016). However, most of our knowledge on seed dispersal by megafauna comes from studies on elephants (Campos-Arceiz et al., 2008; Poulsen et al., 2018, 2021; Tan et al., 2021), creating potential biases in our understanding of megafauna and their seed dispersal roles. Rhinos, for example, exhibit differences in physiology, diet and ranging behaviours compared to elephants (Dinerstein and Wemmer, 1988; McConkey et al., 2022a). To determine whether comparisons between elephants and smaller animals can be extrapolated to megafauna, generally, we require empirical data on a wider range of megafauna.

A lack of knowledge on the potentially distinctive roles of different megafaunal species has implications for our understanding of the dispersal, evolution and future of megafaunal-syndrome fruits. These fruits are very large (> 40 mm wide) and are considered to be reliant on megafauna for effective dispersal, because of the inefficient seed handling and dispersal by non-megafaunal animals (Janzen and Martin, 1982; Chapman et al., 1992; Dinerstein and Wemmer, 1988; Guimarães et al., 2008; McConkey et al., 2022b). Most of our empirical evidence on seed dispersal of megafaunal fruits come from elephants, or from regions where megafauna are now extinct (Jansen, et al., 2012; McConkey et al., 2018; Muñoz-Concha et al., 2022; Blanco et al., 2019; Zaya and Howe, 2009) and, consequently, we lack the empirical evidence to fully understand how effective different megafaunal species might be in seed dispersal of these very large fruits.

In the grasslands and forests of Nepal, the greater one-horned rhino (*Rhinoceros unicornis*) functions as a megafaunal seed disperser (Dinerstein and Wemmer, 1988), sharing habitats with Asian elephants (*Elephas maximus*), and often wild and domesticated bovids (Ahmad et al., 2020). Once widely distributed, the greater one-horned rhino is now critically endangered and ecologically extinct in many regions (Mahmood et al., 2021). In the riverine forests of southern Nepal, trees of *Mallotus nudiflorus* L. (family Euphorbiaceae), Kulju & Welzen (formerly named *Trewia nudiflora* L.) are heavily reliant on the greater one-horned rhino for dispersal (Dinerstein and Wemmer, 1988; Dinerstein, 2003). *Mallotus nudiflorus* fruits are large, enclosed in a tough endocarp, and become dull-coloured when ripe, thereby displaying a megafauna dispersal syndrome, although elephants do not consume them (Dinerstein and Wemmer, 1988). The fruits of *M. nudiflorus* are consumed and dispersed by deer and domestic bovids, but are infrequently consumed by monkeys. Further, the dispersal and germination of these fruits may be facilitated by flood waters and being trampled (crushed) by the feet of rhinos and elephants might also assist dispersal and germination (Dinerstein and Wemmer, 1988; Khadka and Lamichhane, 2020). This scenario provides an opportunity to investigate seed dispersal of a megafaunal fruit by a megafauna other than elephants, and also to assess whether domestic bovids can contribute to seed dispersal.

The main objective of this study was to compare the quality of seed dispersal achieved by rhinos and domestic bovids (buffalo and cattle) for *M. nudiflorus*. To assess quality, we measured seed dispersal distances achieved by rhinos and bovids, compared the duration of seed passage in rhinos and bovids, and evaluated the impact of gut passage on seed germination. Germination tests were conducted on other identified seed dispersal modes (regurgitation by deer, dropped by monkeys, water) and fruit fates (uneaten, rotten, crushed) for further comparisons. These tests were done in both riverine forests and grasslands, representing the two main habitats where *M. nudiflorus* is found. We propose the following hypotheses: 1) The gut passage time for *M. nudiflorus* seeds through rhino will be longer compared to bovids due to differences in gut physiology and body size. 2) Rhinos disperse seeds over longer distances than bovids due to their longer gut passage time and larger home range. 3) Seed germination of *M. nudiflorus* will be more likely after passage through rhino guts, compared to other dispersal modes.

2. Methods

2.1. Study sites

The study was carried out in two national parks within the Terai Arc Landscape in Nepal: Chitwan National Park (CNP) and Shuklaphanta National Park (ShNP). CNP (latitude 27°16.56′–27°42.14′N; longitude 83°50.23′–84°46.25′E) has a core area of 953 km², a buffer zone spanning 729 km², and elevation ranging from 110 to 850 m above sea level (Subedi et al., 2017). The climate in CNP is subtropical monsoonal, characterized by three distinct seasons: monsoon (July–October), cool-dry (November–February), and hot-dry (March–June). The average annual temperature ranges from 8°C in January to 36°C in April. The park receives an average annual rainfall of 2036 mm, with more than 80 % occurring during the monsoon season (Subedi, 2012). ShNP (longitude 80°06′04″ and 80°21′40″ E, latitude 28°45′16″ and 28°57′23″ N) covers a core area of 305 km², a buffer zone of 243.5 km² and has an altitude range of 174–1386 m asl. In contrast to CNP, ShNP experiences a drier climate, with an annual rainfall between 1800 mm (Subedi, et al., 2013).

Both parks exhibit similar vegetation types and mammal populations (Subedi, 2012). In ShNP, both feral and domestic buffalo and cattle are commonly observed, often venturing deep into the park during the day and returning to nearby villages for shelter at night (B. Awasthi unpublished data). The feral cattle group inhabits the forest, with occasional visits to the villages for salt and specific nutrients. In CNP, domestic buffalo and cattle are not as commonly observed (as in ShNP), but can venture deep into the park; gaur (*Bos gaurus*) – a wild bovid – also occurs in CNP at relatively low density (0.3 gaur km⁻² in 2011) (DNPWC, 2020). Rhinos have an established population in CNP where they have always occurred, while they have been reintroduced to ShNP and occur at low density (~0.03 rhinos km⁻²) (NTNC, 2021).

2.2. Study species

Mallotus nudiflorus Linn (Euphorbiaceae) is a dioecious tree that is characterized by its fast growth and early successional nature. It typically thrives in moist environments with high light exposure (Chaurasia and Shukla, 2018), and predominantly occurs in the riverine forests of both parks, but is also found in grasslands. This species is found in Nepal, India, Malaysia, and the southern regions of China, where it is prized by humans and used for multiple purposes (DFRS, 2014). *M. nudiflorus* fruit become available during the monsoon season (April - October). Once fully ripe, the fruits undergo a slight colour change and fall to the ground (Dinerstein and Wemmer, 1988; Awasthi, 2024). Fruit diameter averages 41.53 ± 3.24 (mean, SD) and fruits contain a mean of 3.5 seeds, with an average diameter of 7.8 mm (Awasthi, 2024, Dinerstein and Wemmer, 1988). *M. nudiflorus* is shade-intolerant; despite abundant fruit fall and successful seed germination, seedling recruitment is poor under the forest canopy (Dinerstein and Wemmer, 1988).

2.3. Feeding trials with rhinos and domestic bovids to determine gut passage rates and proportion of seeds dispersed intact

2.3.1. Selection of animals for trials

Feeding trials were conducted with *M. nudiflorus* fruit fed to rhinos, cattle, and buffaloes. Three male adult rhinos aged between 16 and 32 years were fed at the Central Zoo in Lalitpur, Nepal in August and September 2021. A one-year-old semi-captive orphaned rhino (female) was opportunistically included in the trials, due to its presence at the National Trust for Nature Conservation (NTNC)'s Biodiversity Conservation Center (BCC) at Sauraha, Chitwan in August and October 2020. Feeding trials with domestic bovids were conducted at ShNP in August and September 2020. The trials included domestic cattle (3 males, 1 female) (*Bos primigenius*), and two domestic buffaloes (2 females) (*Bubalus bubalis*), ranging in age from five to 16 years.

Feeding trials were attempted with four deer species (barking deer (*Muntiacus vaginalis*), spotted deer (*Axis axis*), sambar deer (*Rusa unicolor*), hog deer (*Axis porcinus*) but the deer refused the fruit even though wild individuals consume *M. nudiflorus* fruit. Wild water buffaloes (*Bubalus arnee*), and elephants were not tested but both refused the fruit and they have never been noted to consume the fruit in the wild (Appendix S1: Protocol of feeding trials).

Table 1

Fruit consumed and gut retention time and proportions for captive rhinos, buffaloes, and cattle fed *Mallotus nudiflorus* fruit.

		Adult rhino	Juvenile rhino	Cattle	Buffaloes
Experimental details	No. Trials	4	4	6	3
	No. Trials/individuals	¼	4	1	1
	Number of fruits given	100	100	100	100
Number of fruits consumed	Mean number of fruit/indiv (± sd)	45 (6.67)	24.75 (10.20)	36.5 (5.58)	34 (3.55)
	Range	28–69	12–55	14–56	26–42
Number of seeds swallowed	Mean number of seeds/indiv (±sd)	155.7 (29.84)	85.64 (35.10)	126.29 (19.24)	114.18 (17.28)
Gut retention time, GRT (hours)	Mean appearance of first seed (h)	47.99 (7.29)	42.29 (3.89)	31.18 (6.33)	28.67 (2.51)
	Mean GRT by seed (±sd)	89.02 (4.21)	69.70 (4.30)	59.33 (10.25)	60.82 (3.37)
	Mean GRT by individual (±sd)	88.75 (2.1)	69.70 (4.30)	60.13 (10.25)	60.89 (3.37)
	Mean max GRT(±sd)	158.47 (4.38)	108.81 (17.16)	105.69 (9.42)	103 (4.92)
	Maximum (±sd)	163.24	132.29	115.21	108.5
Gut passage Proportion (GPP)	Mean (±sd)	0.52 (0.09)	0.45 (0.22)	0.40 (0.14)	0.30 (0.025)
	Minimum-Maximum	0.45–0.64	0.20–0.72	0.23–0.57	0.28–0.33

2.3.2. Execution of feeding trials

Before and during the feeding trials, the only modification made to the diets of the animals was the inclusion of *M. nudiflorus* fruit ([Appendix S1. Protocol of feeding trials](#)). A 15-day gap separated each trial if the same individual was used for multiple feeding trials. Due to logistical constraints, trials for different animal species were not always conducted simultaneously. In each feeding trial, a specific quantity of fruits ([Table 1](#)) was provided to each individual. The estimated number of seeds consumed was calculated by multiplying the mean number of seeds per fruit (3.47) by the number of fruits consumed. Afterward, all excrement was collected to recover intact and crushed seeds, for estimation of seed survival rates and gut passage times. In each trial, the fruits were offered to the animals during daylight hours, one hour before their regular feeding time. The animals were given a maximum of 60 minutes to consume the fruits, except for cattle which were given three hours during one trial and, in one instance, left overnight for a total of six hours. Uneaten fruits and dropped seeds were collected and counted.

2.3.3. Collection of faeces and seeds

Data on defecation time were collected using camera traps and closed-circuit television (CCTV) for rhinos. Dung collection commenced five hours after ingestion of the first fruit for bovids, and the following day for rhinos. For bovids the collection of faeces was performed every three hours and for rhinos every six hours including through the night, with the time of collection recorded. The dung piles were thoroughly examined by hand using surgical gloves; pressurized water was used to separate defecated seeds from the dung. Faecal collection was discontinued if no seeds were retrieved for three consecutive days. Feeding behaviour monitoring protocols for rhinos were based on a study by [Dinerstein and Wemmer \(1988\)](#), while those for cattle and buffaloes followed the methods outlined by [Sekar et al. \(2015\)](#) ([Appendix S1: Protocol of feeding trials](#)).

2.4. Seed germination experiments

We assessed the germination success of eleven dispersal modes (seeds defecated by rhino, gaur (a wild bovid, *Bos gaurus*), cattle, and buffalo, seeds regurgitated by deer, seeds dropped by monkeys, fruit crushed by the feet of rhinos and elephants, water-dispersed (collected from forest floor after flooding), seeds in uneaten/rotten fruit), and two control conditions (cleaned seed, whole fruit) ([Table S3](#)) under natural conditions. We included all potential dispersal modes identified during field studies ([Awasthi, 2024](#)), to account for all possible ways in which seeds could establish successfully. This included intact seeds in otherwise rotten fruit pulp, those fruits crushed by megafauna (thereby releasing the seeds) and rare modes such as inefficient handling by monkeys.

Seeds were germinated in 10 × 10 m plots in each habitat type (grassland, and riverine forest) and in each park, and were fenced to prevent disturbance from grazing animals ([Appendix S2](#)). The top layer of soil (depth of 10 cm) was inverted for the experiment, to reduce the quantity of seeds from the soil seed bank. Experiments were carried out between August and October 2020, which coincided with the fruiting season of *M. nudiflorus*. Each of the eleven dispersal and control modes was replicated 3–4 times in different seedling bags with each replication involving the sowing of 20–30 seeds under different dispersal conditions. Seeds were collected from the feeding trials as well as from the field. The four treatments involving defecated seeds were planted with and without dung, while the other treatments were planted in soil only to replicate the natural state. Detailed descriptions of these treatments are provided in [Appendix S2: Protocol of seed germination](#).

Throughout the 60-day experiment, the seeds were monitored every 3–5 days and were watered if the soil was dry; germination was done under natural light and temperature conditions. To avoid double counting, germinated seeds were left in the experiment for 2–3 days before removal. After 60 days, ungerminated seeds were considered unviable, following the protocol by [Dinerstein and Wemmer \(1988\)](#). We calculated the proportion of the seeds that germinated and the germination speed; results on germination speed can be found in [Appendix S3](#) (see [Appendix S3](#). Germination percent and germination rate)

2.5. Calculation of seed dispersal distances for rhinos and bovids

2.5.1. Movement data for rhinos and bovids

Movement data for rhinos were used from a prior study ([Subedi, 2012](#)) and combined with gut passage rates to enable calculations of seed dispersal distances. Movement data were gathered from four individuals (2 males, 2 female) equipped with GPS collars in 2011 in CNP. Detailed capture and collaring procedures can be found in [Subedi \(2012\)](#). The GPS collar devices were set to record rhino locations every 30-minute intervals for 24 hours, but we used data collected at six-hour intervals (to match gut passage collection data) to analyse seed dispersal distances. Data on rhino movements were obtained from July to November, 2011, to coincide with the peak fruiting season for *M. nudiflorus*.

In ShNP, movement data for cattle (3 individuals: one from a domestic herd from Bagphanta village and two from feral herds) and buffaloes (2 individuals; domestic herds from Bagphanta village) were collected using handheld GPS devices. Domestic herds (2–5 individuals that moved as a group) were monitored by selecting one individual tagged with a rope and bell. The movements of the individuals were followed from sunrise to sunset for five to seven days, repeated four times between August and September 2020 (two months).

Two feral cattle herds (>250 individuals) residing in the core area of the park were also observed. Two individuals were tagged, but they predominantly grazed with the herd in the park's grassland, spending most of their time near the Chaudhar Riverbanks. Observations were limited to daytime, potentially missing any unusual movements occurring at night.

2.5.2. Seed dispersal distance estimation

Seed dispersal distances achieved by rhinos were calculated using the gut passage times and movement data as noted above. Initially, the recorded locations were imported into Google Earth Pro for visualisation. For each individual rhino, 42–90 different starting points were used and these were randomly sampled (Westcott et al., 2005; Campos-Arceiz et al., 2008) within the riverine forest, where *M. nudiflorus* is commonly found. Rhino displacement was measured every six hours until the gut passage time was completed (163 hours); a total of 278 displacements were obtained.

The net displacement of rhinos was represented by the distance between the initial and final GPS positions. Two matrices were created: one showing the displacement between each pair of points using the Distance Matrix Tools in QGIS, to calculate the distance from the initial point to each subsequent point, and the other representing the time elapsed between each pair of points, calculated using Excel. These matrices produced displacement-versus-time curves (Westcott et al., 2005; Campos-Arceiz et al., 2008; Seker et al., 2015).

GPS coordinates were imported into Google Earth Pro for visualisation and the Distance Matrix Tools in QGIS used to calculate the distance between the starting point and subsequent point, to generate displacement curves for bovids in a similar way as for rhinos (see above). Eighteen displacement curves were created for buffaloes with a maximum gut retention duration of 108 hours, and 38 displacement curves were created for cattle with a maximum gut retention duration of 115 hours.

A mechanistic seed dispersal curve was developed using seed retention times from captive trials with rhinos, cattle, and buffaloes, along with their movement patterns, to estimate dispersal distances (dispersal kernels) (Campos-Arceiz et al., 2008; Sekar et al., 2015). The percentage of seeds retained in the gut was estimated each six-hour interval to match the displacement distances measured for rhinos, cattle and buffaloes. These data were used to create displacement curves illustrating the frequency of seed deposition at increasing distances, allowing for the estimation of seed dispersal distance based on movement data.

2.6. Data analysis

All statistical analyses were performed in the R statistical environment (version 3.4.0, R Core Team 2023). Data visualization was performed using the *ggplot2* package (Wickham, 2016), and functions available in base R. Visualizations of gut retention times were generated using the *Vioplot* package in R (Adler et al., 2024). Prior to analysis, we checked the data for heteroscedasticity and normality, to ensure that assumptions were met. We fitted general linear mixed models (GLMMs) to investigate the gut retention time and gut passage proportions (GPPs) of ingested seeds between species, with feeding trial number considered as a random factor to

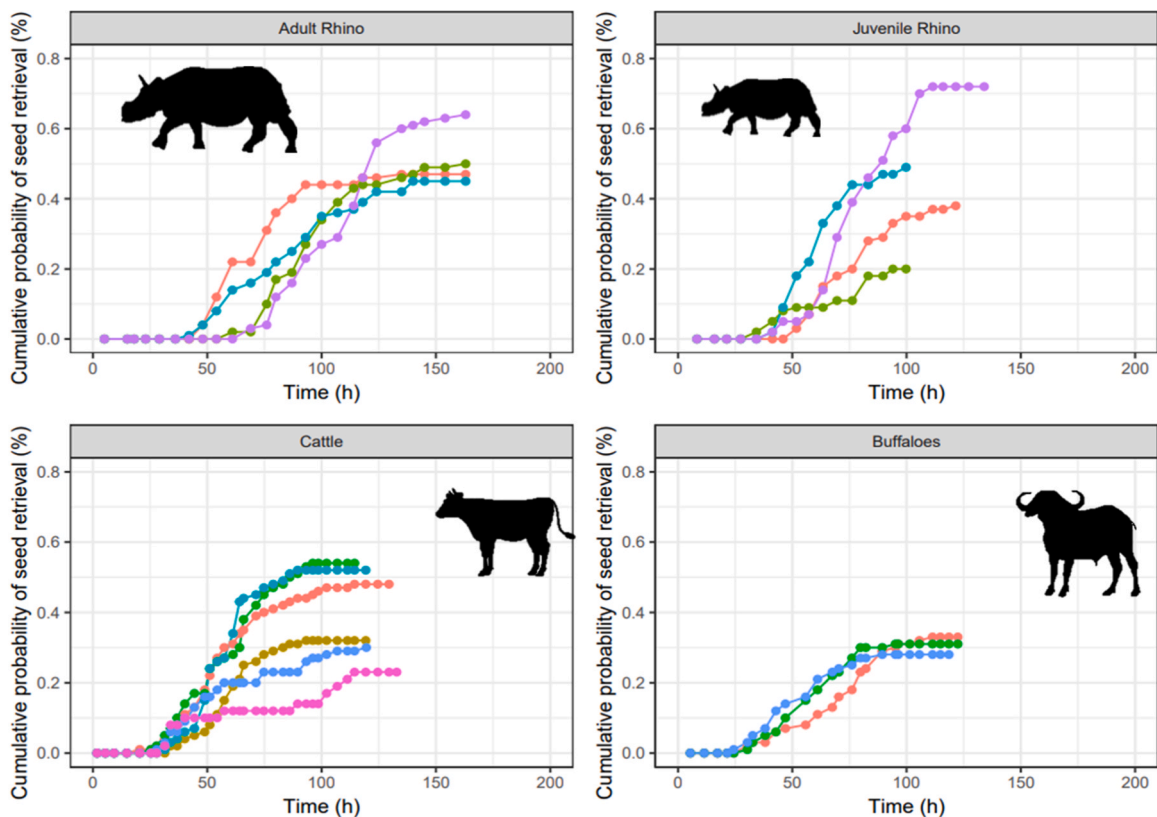


Fig. 1. Cumulative retrieval of ingested *Mallotus nudiflorus* seeds in different individual animals (each individual represented by a different colour) (adult rhino (n = 4), juvenile rhino (n = 4), cattle (n = 6), buffaloes (n = 3)).

control unmeasured variation effects using the *lmer* function of the lme4 package (Bates et al., 2015).

To determine the germination percentage, the following formula was utilized: germination percentage (%) = $(N/S) \times 100\%$, where N represents the total number of germinated seeds and S is the total number of seeds or fruit sowed (Shikang et al., 2015). We used GLMMs with binomial error distribution and logit-link function to assess the impacts of site, habitat, and treatment on germination percentage; replication was considered as a random factor. Except for rhino when examining for other dispersal modes, tests were done for CNP and ShNP separately due to a different subset of animal dispersers and the potential for inter-site differences. Multiple comparisons of means with Tukey Contrasts were used to compare between types of seeds and fruits. The test was adjusted using the Bonferroni method (Hothorn et al., 2008).

Dispersal distances of cattle, buffaloes, and rhinos were evaluated using a GLMM. The response variable was the dispersal distance (obtained from the mechanistic model) of each animal for *M. nudiflorus*, while species was the fixed effects animal ID was the random effect in our model. In addition, to understand the differences of seed dispersal distance among individual animals, animal ID was used as a fixed effect in models. Histograms illustrating the distribution of seed displacements for each animal-*M. nudiflorus* pair was generated using R.

3. Results

3.1. Gut retention time of captive rhinos, cattle, and buffaloes

We found considerable differences in the animals' interest to consume fruits of *M. nudiflorus*, both within and among the three animal species (Table 1). Adult rhinos consumed the most available fruit followed by cattle and buffaloes, and most variation among individuals was displayed by juvenile rhinos and cattle.

Rhinos passed the highest proportion of intact *M. nudiflorus* seeds (Table 1) through their digestive system. The values for adult (0.52) and juvenile rhino (0.45) were not significantly higher than the values for cattle (0.40) and buffaloes (0.30) ($F = 1.729$, $p = 0.1603$). However, greater consistency in the results among trials was noted in adult rhinos and buffaloes, while juvenile rhinos (one individual) and cattle (six individuals) showed variability in GPP among trials (Fig. 1). Broken seeds were also found in the faeces of adult rhino, juvenile rhino, cattle and buffaloes but these could not be quantified.

GLMM testing the gut retention times (GRTs) among different species showed differences in GRTs among the animal groups tested ($F = 12.441$, $p < 0.001$). Adult rhinos had significantly longer GRTs compared to the juvenile rhino ($t_{(553)} = -1.827$, $p = 0.068$), buffaloes (slope = -23.820 , SE = 6.364, $t_{(553)} = -3.743$, $p < 0.001$), and cattle (slope = -29.652 , SE = 5.149, $t_{(553)} = -5.759$, $p < 0.001$) (Table 1, Fig. 2). The GRTs for adult rhino were around 29 h longer than for cattle and buffaloes, and more than 50 h longer

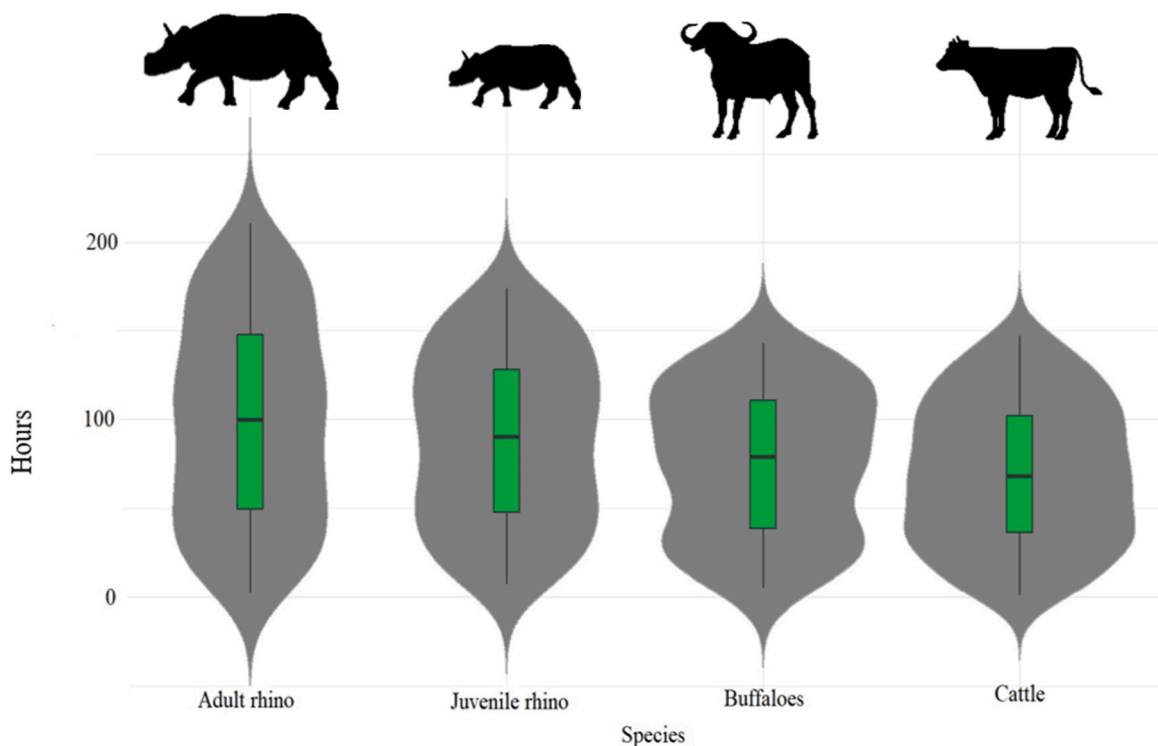


Fig. 2. Gut retention times of *Mallotus nudiflorus* seeds consumed by adult ($n = 335$ seeds) and juvenile ($n = 138$) rhinos, buffaloes ($n = 114$) and cattle ($n = 322$). Adult rhinos had significantly longer GRTs than other species and age-groups.

when considering maximum values (Table 1).

3.2. Seed germination comparisons among dispersal modes, habitats and location

Percentage of seeds germinating after passage through rhinos was not affected by site ($Z = -1.318$, $p = 0.1875$), habitat ($Z = 1.841$, $p = 0.0656$), or dung presence ($Z = 1.667$, $p = 0.0955$), and averaged 78.61 ± 9.82 (mean \pm SD) across all treatments. Other

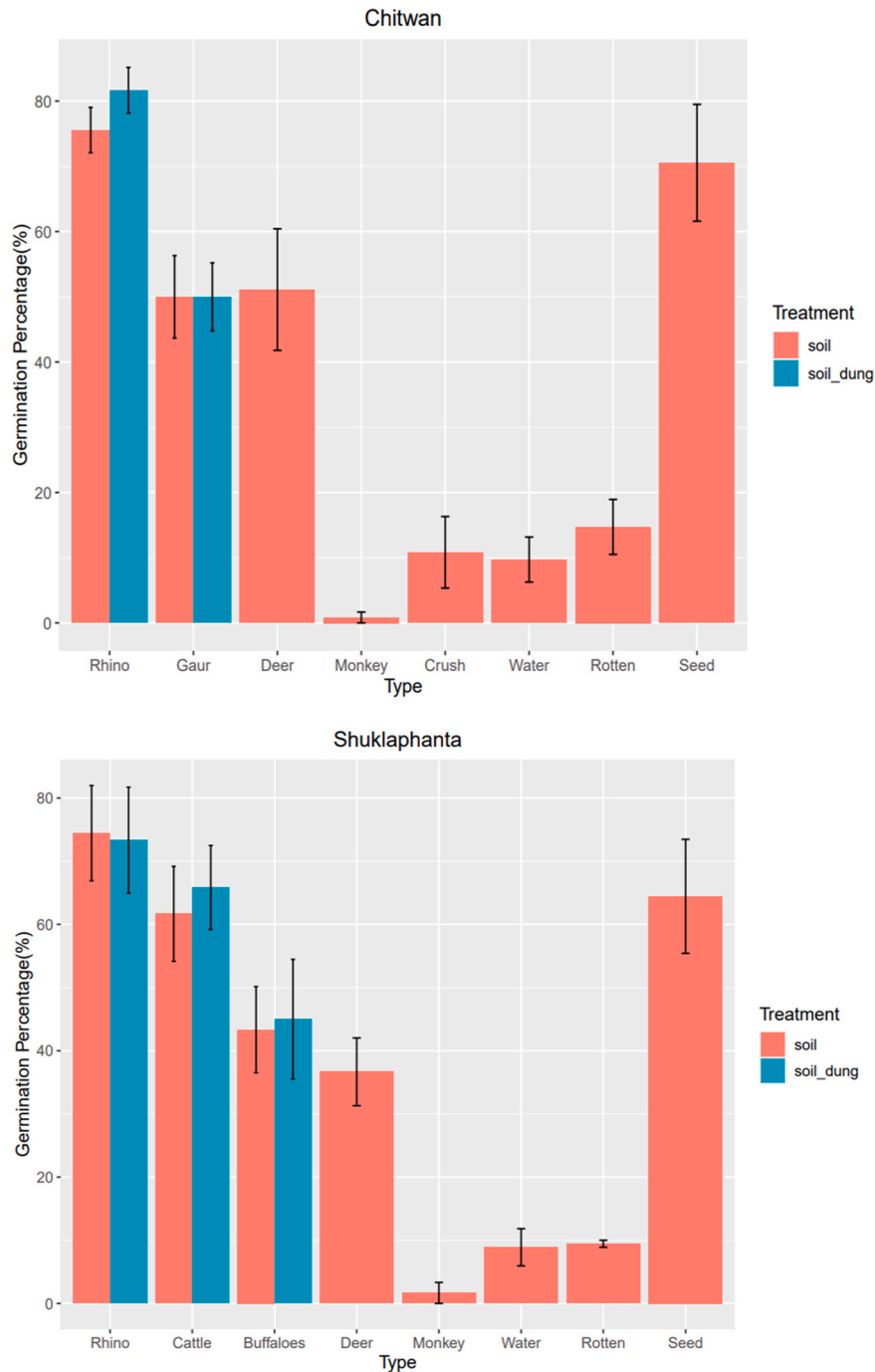


Fig. 3. Germination rate (%) of different dispersal types and the control (seed) in Chitwan National Park (top) and Shuklaphanta National Park (bottom). Types: Rhino = Rhinos gut passed seed, Gaur = Gaur gut passed seed, Deer = Deer regurgitate seed, Monkey = Monkey bitten fruit, Water = Water dispersed seed, Crush = Crushed fruit, Rotten = Rotten fruits, Seed = Seeds without fruit pericarp.

comparisons (below) were conducted for each site due to a difference in the bovid species present.

For endozoochoric dispersers (rhinos, gaur) in CNP, neither habitat ($Z = 1.091$, $p = 0.275$) nor treatment influenced seed germination percentage ($Z = 1.09$, $p = 0.275$). Disperser type (rhino vs gaur) significantly affected germination, with rhino-dispersed seeds having a 1.5 times greater likelihood of germination than gaur-dispersed seeds (slope = 1.291, SE = 0.1823, $Z = 7.082$, $p < 0.001$). Similarly, in ShNP, only disperser type affected the percentage of seeds germinating (among endozoochoric dispersers: rhinos, cattle, and buffaloes), with no effect of habitat ($Z = 1.435$, $p = 0.152$) or treatment ($Z = 0.102$, $P = 0.919$). Rhinos (slope=1.319, SE = 0.246, $Z = 5.344$, $p < 0.0001$) and cattle (slope = 0.808, SE = 0.227, $Z = 3.559$, $p = 0.0004$) had significantly higher germination percent than buffaloes.

In CNP, the comparison among all dispersal types (planted in soil only), indicated that habitat did not have a significant effect on germination rate ($Z = 0.748$, $p < 0.454$), but dispersal type did ($F=29.805$, $p < 0.0001$). Similar results were found in ShNP, with no effect of habitat on germination rate ($Z = 1.912$, $p = 0.056$), but dispersal type had a significant effect ($F = 29.753$, $p < 0.0001$).

Results from the Tukey Contrasts analysis to investigate differences among dispersal types revealed similar patterns across both sites (Table S4 and S5). The highest germination percentages were found for endozoochoric dispersers (rhino, cattle, buffalo, and gaur, in that order) as well as for the control condition (seeds from fruit) (Fig. 3). Rhino-dispersed seeds also exhibited significantly higher germination rates compared to seeds from gaur and buffaloes but did not significantly differ from the cattle-dispersed seeds. Seeds dispersed through deer regurgitation showed higher germination potential than other dispersal types (i.e., monkey bitten fruit, water dispersed seed, crushed fruit, rotten fruits), but these were consistently lower than the endozoochoric dispersers and control condition (Fig. 3). All other dispersal types displayed consistently low germination potential with no statistically significant differences among them.

3.3. Displacement distances and estimates of seed dispersal distances

Rhinos generally covered greater distances compared to cattle and buffaloes (Fig. 4). On average, after 50 hours, the average displacement of rhinos (1.5 km) exceeded the maximum displacement observed in buffaloes and cattle. Domestic buffaloes did not venture beyond a maximum of 1.4 km from their initial location within that time frame, while cattle moved slightly farther (up to 1.8 km) than buffaloes. Domestic buffaloes and cattle tended to return to a resting spot near their owner's village almost every night. In contrast, feral cattle travelled longer distances compared to domestic herds, possibly because they did not have to return to their owner's vicinity (maximum distance of 2.3 km). Overall, domestic bovids displayed repetitive movement patterns, consistently revisiting specific locations for several consecutive days. Transition to new foraging areas occurred gradually over several weeks.

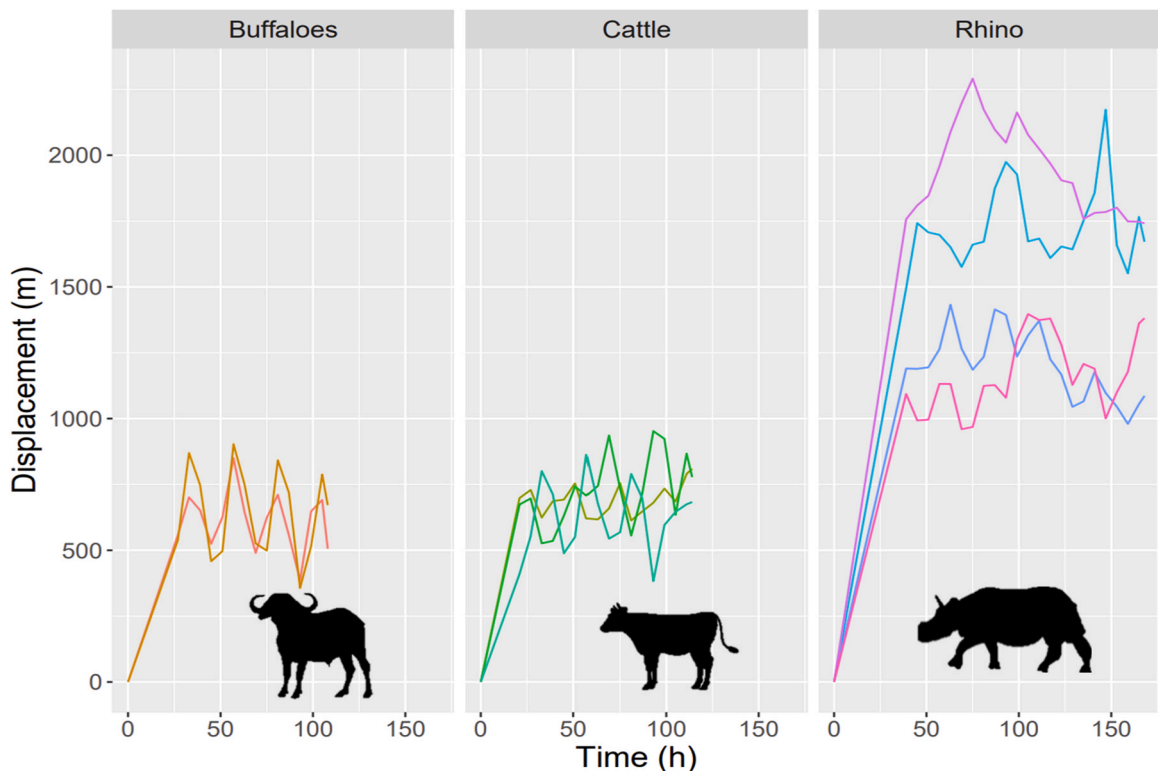


Fig. 4. Mean displacement curve of buffaloes (seed retention time range: 26–108 h), cattle (seed retention time range: 21–115 h), and rhino (seed retention time range: 39–166 h). Different coloured lines represent different individuals.

On average seed dispersal distances were longer for rhinos (mean \pm SD), 1524 ± 984 m; maximum value = 5388 m; median = 1300 m), as compared to cattle (690 ± 387 m; maximum, 2216 m; median = 650 m) and buffaloes (635 ± 310 m; maximum = 1371 m; median = 670 m) (Fig. 4). Differences in dispersal distances were statistically significant among species ($F = 8.737$, $P = 0.011$). These differences were significantly higher in rhinos (slope = 886.495, SE = 277.527, $t_{(8.615)} = 3.194$, $p = 0.0116$), as was the variation in dispersal distances among individual rhinos ($F = 91.789$, $P = 0.011$). However, there was no significant difference between the dispersal distances of cattle and buffaloes ($t_{(7.541)} = 0.180$, $p = 0.86$). Overall, rhinos dispersed around 80 % of swallowed seeds more than one kilometre, compared to 20 % for cattle and 15 % for buffaloes.

4. Discussion

This study provides the first comprehensive analysis of seed dispersal distances by rhinos, a megafaunal taxa. Greater one-horned rhinos dispersed *M. nudiflorus* seeds up to a maximum distance of ~ 5.4 km, with an average distance of 1.5 km and notable variations in movement rates among individual rhinos. Domestic bovids coexisting in the same habitat were also effective dispersers of *M. nudiflorus* fruits, as they consumed many fruits and enhanced the germination rate of seeds passing through their digestive system. However, our findings indicated that domestic bovids cannot completely substitute the long-distance seed dispersal role that rhinos provide for *M. nudiflorus* seeds.

Domestic bovids are conspicuous and relatively new elements in some rhino habitats, and they also feed on *M. nudiflorus* fruit (Dinerstein and Wemmer, 1988). However, they dispersed seeds less than half the distance of rhinos, and only 15–20 % of seeds were moved beyond one kilometre, compared to 80 % for rhinos; the likelihood of germination was also reduced for bovids. Cattle and buffaloes exhibit limited movements and primarily grazed in designated feeding areas, with even feral cattle only shifting to new foraging areas over a period of weeks. Consequently, seeds ingested by the cattle and buffaloes are frequently found near to their original site of consumption, as also documented in India in a comparison between the dispersal roles of elephants and domestic bovids (Sekar et al., 2015).

In contrast to bovids, rhinos displayed a broad range of movement behaviors, sometimes staying close to their initial location for extended periods, while at other times moving five kilometres in a single day, thereby facilitating regular long-distance seed dispersal.

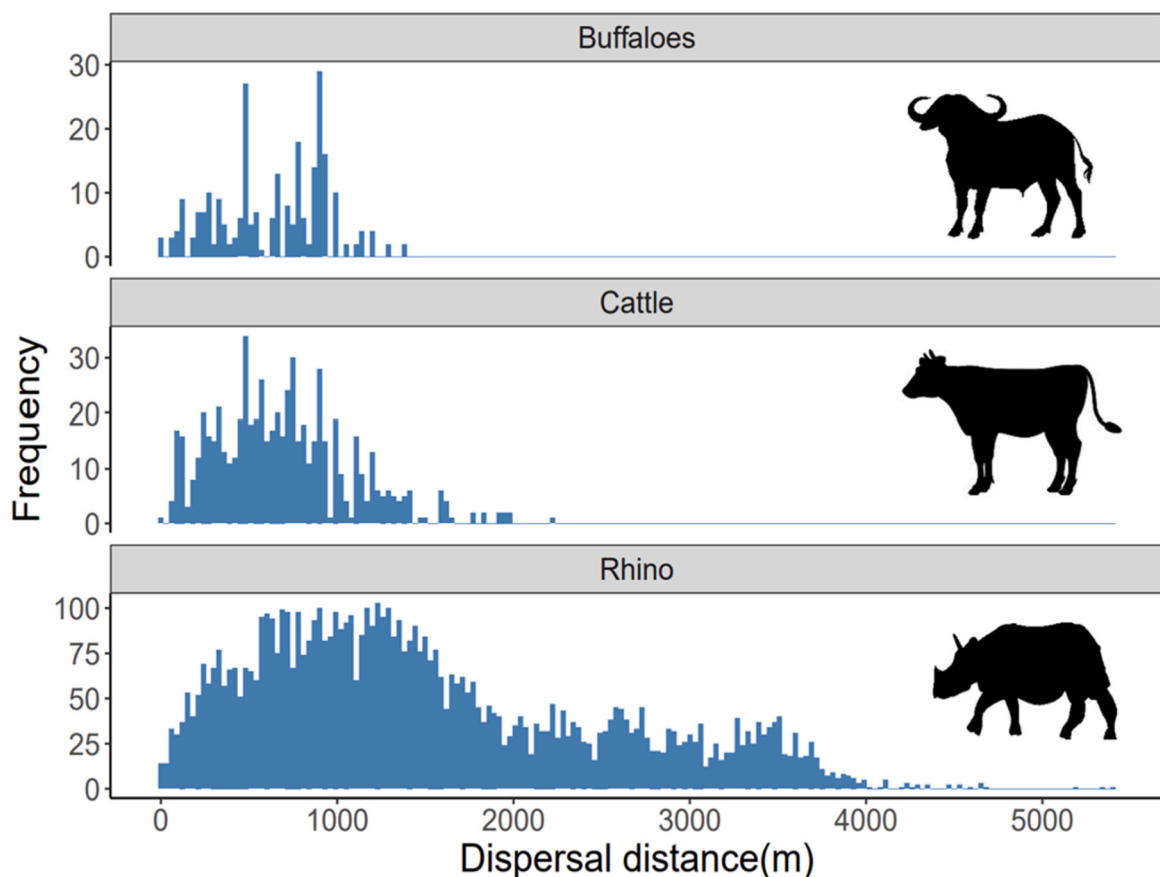


Fig. 5. Seed displacement histogram of buffaloes (top), cattle (middle), and rhinos (bottom). Bovid movements were measured using a handheld GPS, while rhino movements were derived from radio-telemetry data.

In landscapes where rhinos are absent, there will be a decrease in the frequency of long-distance seed dispersal. This will have consequences for the connectivity of *M. nudiflorus* populations and spatial patterns of genetic diversity (Pires et al., 2018). However, in habitats where bovids are present, the effect will be less pronounced compared to habitats without them. The extensive movements of rhinos also enable *M. nudiflorus* seeds to reach the diverse habitats in which the trees are located. Seed germination was not influenced by habitat, but the prevalence of *M. nudiflorus* in riverine forests suggests differential survival at some life stage. The persistence of *M. nudiflorus* trees across the landscape and in diverse habitats offers important food sources for rhinos and other herbivores. The restricted movements of domestic bovids suggest they are an incomplete substitute for rhino seed dispersal, but they may help sustain *M. nudiflorus* recruitment in disturbed habitats where rhinos, and potentially other wild seed dispersers, are absent or scarce.

Our study highlights important similarities and differences in the seed dispersal roles of megafaunal rhinos and elephants. Like elephants, we confirmed that rhinos are also long-distance seed dispersers, although elephants disperse seeds over longer distances. Asian elephants disperse seeds 3.5 km on average (twice that of rhinos), with a maximum of 6 km (Campos-Arceiz et al., 2008; Sekar et al., 2015). The rhinos were similar to elephants in only passing a proportion of the swallowed seeds intact. Similar to results from Dinerstein and Wemmer (1988) for rhinos and *M. nudiflorus*, we found that around 50 % of seeds estimated to be ingested were probably destroyed, which is within the range recorded in elephants (Campos-Arceiz et al., 2008; Sekar et al., 2015; Harich et al., 2016) and is probably largely plant-species dependent. Some Asian rhinos share habitats with another perissodactyl, the Malayan tapir (*Tapirus indicus*); in comparison to tapirs, rhinos probably pass more seeds intact and disperse seeds over longer distances (3.3 km maximum for tapirs; Campos-Arceiz et al., 2012). These comparisons suggest important differences in the seed dispersal roles of extant megafaunal species, indicating that reductions in diversity of megafaunal species within a habitat can have consequences for the dispersal and recruitment of fruits. The disappearance of rhino species from Asian ecosystems will influence the diversity of plant species dispersed by megafauna (for example, elephants do not feed on *M. nudiflorus*) and the range of distances and specific microhabitats to which seeds are dispersed (McConkey et al., 2022a).

M. nudiflorus fruits are very hard, which is a characteristic trait of megafaunal-syndrome fruits (Dinerstein and Wemmer, 1988; Janzen and Martin, 1982; Guimarães et al., 2008). This hardness affects the accessibility of the fruits to other fruit-eating animals and could also contribute to the observed variation among the animals we tested. Monkeys rarely consume *M. nudiflorus* fruits (Awasthi, 2024), and they are inefficient dispersers with lower germination rates even compared to water dispersal or when the fruit are crushed by large animals. The only other wild dispersal vectors of *M. nudiflorus*, besides rhinos, are gaur (wild bovids), which are rare in some habitats and absent in others, and deer (mainly *Axis axis*) (Dinerstein and Wemmer, 1988; Khadka and Lamichhane, 2020). Consumption by both gaur and deer reduced germination rates, compared to rhinos and cattle. Deer, which are abundant in many *M. nudiflorus* habitats, likely play a crucial role as dispersers due to their frequent feeding on *M. nudiflorus* (Awasthi et al., 2024, Awasthi, 2024). However, the hardness of fruits poses a challenge for deer consumption, as evidenced by captive deer refusing to eat the fruits during feeding trials. The variation we observed among captive rhinos and bovid individuals might also be influenced by their willingness to consume hard fruits, as well as other factors such as dental condition, and size (Roth and Shoshani, 1988; Campos-Arceiz et al., 2008; Sekar et al., 2015). Hence, our findings support those of previous studies indicating that megafaunal fruits are most effectively dispersed by megafauna, although other dispersal modes can also provide supplementary services to different degrees (Blanco et al., 2019; McConkey et al., 2015, 2018; Sekar et al., 2015).

A major limitation of our study was our inability to determine the retention time and subsequent dispersal distances of seeds regurgitated by deer, as captive individuals refused to consume the provided fruit. Considering the deer are probably the second most important seed disperser of *M. nudiflorus* (after rhinos and before bovids) (Awasthi, 2024), it is important to investigate whether deer contribute to long-distance dispersal or primarily disperse seeds over short distances. In India, spotted deer retain seeds up to 27 h before regurgitating (Prasad et al., 2006), and most seeds are deposited in resting or bedding sites (Sridhara, 2017), but, spotted deer also make direct longer distance movements of up to 500 m, thereby potentially acting as good seed dispersers. Another unresolved question is why elephants avoid consuming the *M. nudiflorus* fruits in the wild, indicating variations in fruit selection even among megaherbivores (McConkey et al., 2022a). Finally, some *M. nudiflorus* seeds and fruits may be dispersed by secondary dispersers (Awasthi et al., 2024) or by monsoonal floodwaters, offering both short and long-distance dispersal opportunities that are currently undocumented.

5. Conclusions

Domestic bovids can contribute to the maintenance of the megafaunal-fruited *M. nudiflorus* tree populations, similar to the interactions seen with other non-megafaunal animals and megafaunal fruits (Hirsch et al., 2012; Blanco et al., 2019). However, our findings suggest that the dispersal service provided by domestic bovids are limited in terms of the dispersal distances achieved (less than 50 % of that of rhinos), which may reduce the range of sites reached and the likelihood of seed germination. We also report the first seed dispersal distances achieved by rhinos, confirming them as consistent long-distance seed dispersers. Overall, rhinos have similar seed dispersal attributes as elephants (the megafauna for which we have most data); however, there are differences in fruit choices, as indicated by only rhinos and not elephants consuming *M. nudiflorus* fruits. Rhinos were historically the primary seed dispersers in the Terai floodplains over 200 years ago (Dinerstein, 2003), and their disappearance from many regions may have had negative repercussions for the *M. nudiflorus* populations following their extinction.

CRedit authorship contribution statement

Balram Awasthi: Conceptualization, Methodology, Visualization, Investigation, Resources, Project administration. Data curation,

Formal analysis, Writing – original draft, Writing – review & editing. **Kim R. McConkey**: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing, Supervision. **Naresh Subedi**: Methodology, Writing – review & editing. **Babu Ram Lamichhane**: Writing – review & editing. **Sasith Tharanga Aluthwattha**: Writing – review & editing. **Jin Chen**: Conceptualization, Methodology, Visualization, Writing – review & editing, Funding acquisition, Supervision

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03120](https://doi.org/10.1016/j.gecco.2024.e03120).

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